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Introducing tool-based feeders to zoo-housed chimpanzees as a cognitive challenge: spontaneous acquisition of new types of tool use and effects on behaviours and use of space

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Abstract

Cognitively challenging environments are vital to the welfare of captive animals. However, practical enrichment devices that can facilitate animals' natural behaviours and accommodate individual variation are still limited. We created two types of feeders to facilitate tool-using behaviour in captive chimpanzees: pounding and dipping feeders. The pounding feeder was inspired by pestle-pounding behaviour observed in wild chimpanzees, and we expected that chimpanzees would pound soft foods. The dipping feeder was designed to stimulate actions similar to ant-dipping behaviours observed in wild chimpanzees. We investigated (1) how chimpanzees acquire tool-using behaviours and (2) the effects of the feeders on chimpanzee behaviour and use of space. The subjects were five chimpanzees housed in the Kyoto City Zoo, Japan. In study 1, conducted between March and May 2014, we introduced the feeders and examined the chimpanzees' behaviours and the characteristics (length, width, etc.) of any tools they used. In study 2, conducted between September and October 2014, random days were designated when feeders were available (enriched condition) and not available (control condition). In study 1, all adult chimpanzees could use the dipping feeder, and two females could obtain foods from the pounding feeder by hitting the foods several times. The ability to acquire new tool-using behaviours was consistent with ability in existing tool-use behaviours. One infant started to use tools by trial and error. Study 2 showed that under the enriched condition, tool-using behaviours increased, stress-related behaviours decreased, and the use of space changed. These results suggest that these tool-based feeders provided an appropriate challenge for the chimpanzees.

Introduction

Providing cognitive challenges has been recognised as important for animal welfare; such practices are termed "cognitive enrichment" (Clark 2011; Meehan and Mench 2007; Morimura 2006). Recently, Clark (2011) proposed a definition of cognitive enrichment as an approach that "(1) engages evolved cognitive skills by providing opportunities to solve problems and control some aspect of the environment, and (2) is correlated to one or more validated measures of well-being". The provision of cognitive tasks has been reported to improve animal welfare. For example, studies have used puzzle feeders that required hidden food items to be extracted from holes using fingers or tools (Bloomsmith 1988; Clark et al. 2013; Clark and Smith 2013), a juice-dipping feeder that required tool use to obtain liquid from tubes (Celli et al. 2003), and other more artificial computerised devices (Herrelko et al. 2012; Tarou 2004; Whitehouse et al. 2013; Yamanashi and Hayashi 2011). These studies indicated that animals engage in such cognitive tasks voluntarily, and the tasks presented increased species-specific behaviours, decreased abnormal behaviours, and affected social interactions. Although these studies reported the usefulness of such apparatus, the animals may have adapted to these tasks easily. To keep the cognitive component challenging, tasks should be modified and updated regularly, while meeting individual cognitive abilities (Meehan and Mench 2007). Therefore, diverse practical cognitive enrichment interventions that serve the needs of various institutions and individuals are needed.

Promoting natural behaviours among zoo animals is key to improving animal welfare, serving as a central component of *ex situ* conservation and visitor education. Therefore, cognitive challenges that facilitate natural behavioural patterns would be a fitting enhancement to the role of modern zoos. Although implementation of cognitive enrichment has been increasing, most previous cognitive enrichment efforts required the animals to perform a simple manipulation, such as extracting something from a visible hole (e.g. puzzle feeder or pseudo-termite mound) or adapting existing skills to novel devices (e.g. touching a computer screen). However, in wild chimpanzees, the forms of tool use are diverse and sometimes include complex action patterns to obtain food (Humle 2011; Nishida et al. 2010; Whiten et al. 1999). For example, wild chimpanzees in Bossou crack open oil-palm nuts to eat the edible kernel contained inside the hard shell by using a pair of stones (Matsuzawa et al. 2011). Pestle-pounding behaviours, mashing the apical growth tip of the crowns of oil-palms with mature petioles detached from the tree, were also seen at the same study site (Yamakoshi and Sugiyama 1995). Studies have reported that chimpanzees gradually acquired these types of behaviours by observing conspecifics and via individual trial-and-error processes and it sometimes took many years to develop the skills (Hirata et al. 2009; Inoue-Nakamura and Matsuzawa 1997). Therefore, devices that require novel and complex action patterns would be expected to be more challenging for chimpanzees, while increasing the diversity of natural behavioural repertoires.

An important aspect of cognitive enrichment is addressing individual differences in cognitive abilities and preferences (Meehan and Mench 2007). Previous studies have suggested that cognitive performance can differ depending on age, sex, rearing conditions and previous experience (Thornton and Lukas 2012). In the case of chimpanzees, one study investigated the influence of such factors on individual tool-using abilities, as assessed by a reaching tool task (Brent et al. 1995). They found that wild-born individuals were better at the task compared with individuals born in captivity, and other factors did not significantly influence the results. Herrelko et al. (2012) reported that interest in engaging in computerised cognitive research varied depending on personality traits. Considering these individual differences in preferences and abilities, cognitive challenges are not equally useful for all individuals. Thus, it is important to consider individual differences in performance and consistency and inconsistency across different cognitive challenges.

In this study, we examined whether feeders that require tool use can improve the welfare of captive chimpanzees in a zoo environment. We created two types of devices to facilitate tool-using behaviours: a dipping feeder and a pounding feeder. The dipping feeder was designed to stimulate behaviours similar to ant-dipping among wild chimpanzees (Humle 2011), and the pounding feeder was inspired by behaviours seen in wild chimpanzees' pestle-pounding and eating of insect larvae (Matsuzawa et al. 2011). We expected that chimpanzees would pound food to force it through the hole in the bottom of the feeder. These feeders differed in their levels of difficulty and familiarity. The pounding feeders required new motor patterns, such as hitting food several times to force it to the bottom of the device, whereas dipping behaviour was already familiar to the chimpanzees. Additionally, to get the food from the pounding feeder, chimpanzees had to push the food away from them, which has been reported to be difficult for chimpanzees (Mulcahy and Call 2006). Using these feeders, we first investigated the process of behavioural acquisition to assess the appropriate level of challenge and find underlying factors explaining individual tool-use abilities. Then, we investigated the effects of feeders that promoted natural tool-using behaviours on the behaviours of zoo-housed chimpanzees.

Methods

Subjects

The subjects were five chimpanzees living in enclosures connected to both indoor and outdoor compounds in Kyoto City Zoo, Kyoto, Japan (Table 1). The outdoor enclosure was divided into two compounds (200 m^2 each): the east enclosure, a compound with an climbing frame (8 m high) and natural vegetation, and the central ground, a compound with a 7-m-high climbing frame and natural vegetation (Fig. 1a). The chimpanzees were released to the outdoor enclosures every morning, with the timing of their release dependent on the cognitive experiments conducted in their indoor enclosures before release. The details of the cognitive experiments are provided in the methods section of study 1. The chimpanzees were fed seasonal fruits and vegetables for their two meals, and the keepers scattered additional small pieces of fruits and vegetables 2–3 times per day. Before the study periods, the chimpanzees occasionally had access to a dipping feeder in the outdoor enclosure, and they had previously had access to several types of feeders in a former facility where they had lived until 2009 (Kumamoto Sanctuary 2015).

Table 1. Details of chimpanzee subjects.

Name (GAIN number)	Year born	Age at start of study (years)	Sex	Rearing history (number of days with mother)
Suzumi (0556)	1996	17	F	Artificial rearing (4)
Koiko (0281)	1977	37	F	Wild-born
James (0499)	1993	20	M	Mother rearing (2190)
Takashi (0316)	1988	26	M	Artificial rearing (388)
Niini (0737)	2013	1	M	Mother rearing (ongoing)

Note. The order of the individuals corresponds to Table 3. Niini is a son of Koiko and James. All of the adult chimpanzees came from the same research facility in 2009 or 2010 (Morimura et al. 2010; Morimura and Mori 2010). GAIN number represents the registration number in an information network of great apes in Japan (Great Ape Information Network).

Apparatus

The feeders were made from transparent PVC pipe and joints and were attached to the outdoor enclosures (Fig. 1a, b; S1). We created two types of dipping feeders (Fig. 1b), modified from those at Kumamoto Sanctuary (Kumamoto Sanctuary 2015), and filled them with 100% fruit juice diluted with water. To obtain juice from the dipping feeder, chimpanzees soak twigs or other plant materials into the juice and lick the tools. One was a simple bottle created with pipes and caps, and the other was a bottle that had a 30 mm hole in the middle of the PVC pipes.

To obtain food from the pounding feeder, chimpanzees had to hit the food several times to force it to the bottom of the feeder. These chimpanzees had never performed this type of behaviour. Thus, we gradually adjusted the difficulty through three levels depending on each chimpanzee's progress. Differences in hole size determined the level: level 1, 35 mm hole, level 2, 25 mm hole, and level 3, mesh (approximately 15 mm). We put peanuts contained within Chinese cabbage in the level 1 feeder and small (but larger than the hole size) pieces of banana or steamed sweet potato in the level 2 and 3 feeders (Fig. 1b). As the level 3 feeders required both squashing and taking the food from the bottom, they were very difficult for the chimpanzees. We divided this into two behaviours. The level 1 feeder required only repetitive hitting of the food, whereas the level 2 and 3 feeders required that the chimpanzees smash the food to some extent to get it through the hole. We used different types of foods for the different level feeders for practical reasons. We used Chinese cabbage in the level 1 feeder to prevent the food held within it from automatically dropping through the hole. Peanuts were used a

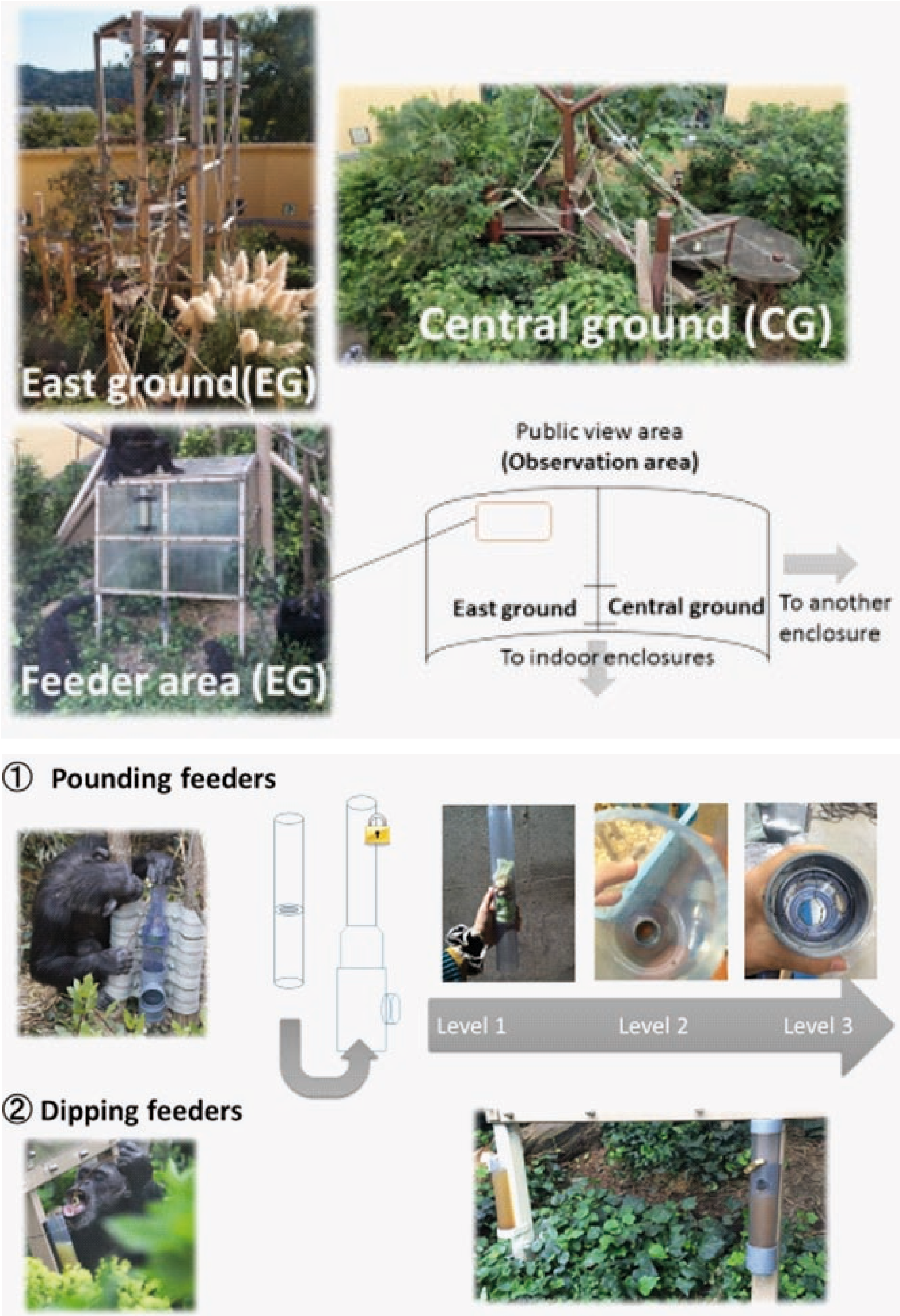

Figure 1. (a) Study sites; (b) details of the two feeders. The difficulty of the pounding feeders could be adjusted by changing the interior tubes (Fig. 1b). The inner containers could be removed for easy cleaning. The size of the holes in the inner tubes differed from those in the first level (full width of the tube, approx. 35 mm hole) to the second level (25 mm hole created using joints) to small mesh (approx. 15 mm). There were two types of dipping feeders. One was a simple bottle created with pipes and caps (left), and the other was a bottle that had a 30-mm hole in the middle of the PVC pipes (right). Figure 1. (a) Study sites; (b) details of the two feeders. The difficulty of the pounding feeders could be adjusted by changing the interior tubes (Fig. 1b). The inner containers could be removed for easy cleaning. The size of the holes in the inner tubes differed from those in the first level (full width of the tube, approx. 35 mm hole) to the second level (25 mm hole created using joints) to small mesh (approx. 15 mm). There were two types of dipping feeders. One was a simple bottle created with pipes and caps (left), and the other was a bottle that had a 30-mm hole in the middle of the PVC pipes (right).

for the level 1 feeder to attract the attention of the chimpanzees because we knew from daily experience that all the chimpanzees liked peanuts.

Materials for tools

The chimpanzees acquired materials for tools from vegetation within their enclosures, where various types of plants were available (Fig. 1a). Vegetation included plants of various lengths and widths. They could freely access all of the vegetation inside the enclosures. Plants were available near the tool-based feeders, and they could also obtain materials at some distance from the feeder locations in the two enclosures (Fig. 1a). We did not provide any other tool materials for this study.

Data collection

The study was divided into two periods: the introduction phase (phase 1: between March and May 2014) and the feeder-assessment phase (phase 2: between September and October 2014). During phase 1, from 30 March to 24 April, one male (Takashi) stayed in the indoor enclosure due to an injury. Additionally, only one compound (east enclosure) was available until 16 April, when gorilla inhabitants were moved to another exhibit. During phase 2, the chimpanzees used both compounds, and no extraordinary event occurred. We placed food and juice in both of the feeders in the morning before the chimpanzees' release to the outdoor enclosures. Both of the feeders were available simultaneously, so the chimpanzees could choose which feeder to use.

Phase 1: Introduction phase

Between March and May 2014, we recorded the chimpanzees' behaviours and tools used with the two types of feeders. In total, we conducted 24 days of observations. We monitored the chimpanzees' behaviours using a video camera (SONY Handycam HDR-CX430) and, occasionally, a digital camera. We observed behaviours from the time the chimpanzees entered the outdoor compound until they finished using the pounding feeders (maximum 2 h if the chimpanzees did not use the feeders). We used two dipping feeders and one pounding feeder until day 16, after which we added one more pounding feeder. Initially, we prepared only the level 1 pounding feeder, and we then used the other levels according to the chimpanzees' progress.

Phase 2: Feeder assessment phase

During September and October 2014, we pseudo-randomly assigned the days when feeders were available (enriched condition: 8 days) and not available (control condition: 7 days). We employed three dipping feeders and two pounding feeders (levels 1 and 3) for the entire study period under the enriched condition. Behaviours were recorded for 2 h, starting when the chimpanzees entered the outdoor enclosures (between 0900 and 1015). We recorded the behaviours (Table 2) and location of all subjects every 3 min by direct observation. To determine changes in the use of space, the east area was divided into ground, tower (a structure located in the middle of the east ground), and the front area (where the feeders were located, approximately 3 × 5 × 2 m^3). The central area was divided into ground and structure (any structure located in the central area). We allocated an equal number of days of cognitive experiments conducted before release and an equal number of weekend days to each condition to minimise the effects of confounding factors.

Behavioural coding and analysis

Study 1: Introducing new tool-based devices

Specific questions were as follows: (1) Which chimpanzees invent pounding behaviours, and how do they do it? (2) Do chimpanzees who acquire new tool-using behaviours share common characteristics? (3) Is there any consistency across different cognitive challenges? (4) How does an infant chimpanzee develop tool-use? (5) What is the appropriate level of challenge? To answer these questions, we analysed the behaviours of the adult chimpanzees during the phase 1 and those of the infant chimpanzee during phases 1 and 2.

Study 1-1: Acquisition and modification of pounding behaviours in adult chimpanzees: The rate of behaviours was coded from video clips during phase 1 by an all-occurrence sampling method, recording each behavioural session from beginning to end using the Observer XT software (Noldus). The ethogram used for the study is shown in Table 2. Tool length and width were recorded both by direct observation and from video and photo data. We calculated tool length based on fist measurements (Lonsdorf et al. 2004) and categorised the diameters into three categories. We also recorded whether chimpanzees obtained tools within reaching distance from the feeders as a measure of flexibility of tool selection. As Takashi was temporarily away from the group and after-effects might have occurred, we used data other than those for pounding feeder use only in March and May. As a result, pounding behaviour acquisition was observed for 20 days, and dipping-feeder use was observed for 10 days.

To check whether cognitive abilities were consistent across different cognitive tasks, we compared the tool-using abilities with performance on numerical sequence tasks (Matsuzawa 2003), conducted 3 or 4 days per week by MT beginning in 2009. Cognitive experiments were conducted sporadically, starting at about 0900, and lasted for about 50 min. In the task, chimpanzees had to touch the numerals that appeared on the touch-panel screen in ascending order. The number of numerals appearing on the screen was adjusted to individual abilities. There were three touch-panel screens, and participation was up to the chimpanzees. Although the participation rate differed among individuals, all of the chimpanzees had an equal opportunity to participate. When one of the chimpanzees came in front of a touch-panel screen, MT provided the task adjusted to that individual's abilities. The details are presented in Tanaka et al. (2015).

Study 1-2: Acquisition and modification of dipping behaviours in an infant chimpanzee: The infant chimpanzee began to show tool-using behaviours between phases 1 and 2. He was first observed dipping juice on 13 September 2014 by MT. To understand the potential relationship between peering (Table 2) and learning, we coded the start and end of the peering behaviours and tool use of the infant from the video clips recorded in phases 1 (20 days) and 2 (8 days) by the all-occurrence sampling method using Observer XT.

To compare the rate of peering between infants and adults, we calculated the rate of peering for each adult by dividing the individual peering rate by the individual's observed rate of tool use. For example, the rate at which individual A peered at individual B (PR_{AB}) was calculated as follows:

$$PR_{AB} = AP_B/T_B$$

where AP_B is the total time that A peered at B, and T_B is the duration of individual B's engaging with the tool-using feeders. Additionally, we divided the infant's tool-use bouts into successes and failures. Success required the completion of three actions: insert a tool into the feeder, remove the tool from the feeder, and put the tool into the mouth. Failure lacked one or more of these actions. To check the relationship between peering behaviours and tool-use success in the infant, we calculated the lag time between the start of peering behaviour and the last bout of tool use (success or failure).

Table 2. Ethogram used in the studies.

Categories	Behaviour	Definition
Studies 1 and 2		
Feeder-related behaviours	Dip	Insert tools into a dipping feeder, remove the tool, and put it into the mouth to get juice.
	Pound	Insert tools into a pounding feeder and hit the food inside the feeder several times to force it out through the hole in the bottom of the feeder.
	Fish	Insert and then remove a tool in an effort to reach the food inside a pounding feeder via the upper part of the feeder.
	Explore feeders	Engage in other activities near the feeders such as checking the contents of feeders, shaking the feeders, and inserting the hands into the feeders.
	Eat	Eat the contents of a pounding feeder after removing them from the device.
	Peer	Look intently at another individual's face, hand, movement, or tools used from a close distance.
	Manipulate object	Manipulate branches in contexts other than feeder use mentioned above.
Study 2		
Normal behaviours	Forage	Search for and eat daily food in the enclosures.
	Remain inactive	Remain immobile.
	Move	Walk, run, or leap on the ground; climb on, swing on, or descend from the structures.
	Perform affiliative behaviours	Engage in affiliative social interactions including social grooming, social play, and social touch.
	Perform aggressive behaviours	Engage in aggressive social interaction including hitting, biting, and charge display.
Stress-related behaviours	Perform self-directed behaviours	Behaviours directed at subjects' own body parts, mainly scratching and self-grooming. Often used as a measure of stress and negative emotion in primates (Baker and Aureli 1997; Leavens et al. 2001; Maestripieri et al. 1992; Yamanashi and Matsuzawa 2010)
	Perform abnormal behaviours	Behaviours never or rarely seen in the wild: regurgitation, faeces smearing, coprophagy, self-slapping, and hair pulling within the study group.

Study 2: Effects of tool-use devices on behaviours and spatial use
Specific questions were as follows: (1) Do tool-based devices decrease stress-related behaviours while promoting natural behaviours? (2) Does introducing the feeders cause chimpanzees to change their use of space? To answer these questions, we compared the behaviours and use of space between control and enriched conditions. We separately analyzed the behaviours of adult and infant chimpanzees.

Statistical analysis

We used a generalised linear model (GLM) and generalised linear mixed model (GLMM) for statistical analysis, using 'R' (ver. 3.2.1; (R Development Core Team 2011). To check whether tool characteristics (length and diameter) for the pounding feeders changed over time, we used the *glm* function, which has a Poisson distribution in GLM. Study phase (four 4-day segments that together constituted the 16 days on which the individual was observed to use the pounding feeders) and feeder difficulty level were included in the fixed factors. We used the *glmer* function with a gamma distribution in GLMM to examine the differences in peering rate between adult and infant chimpanzees. We included the two age categories (adult and infant) as a fixed factor and individual ID as a random factor. We used the *glm* function with a gamma distribution in GLM to analyse whether failure increased peering behaviours. We included the tool-use outcomes (success or failure) as a fixed factor and lag time between the start of peering behaviour and the last bout of tool use as a response variable. We also applied the GLMM to analyse changes in behaviours and use of space following the introduction of the feeders. We used the *glmer* function in the *lme4* package with a Poisson distribution (Bates et al. 2015) or *negbin* in the *aod* package with a negative binomial distribution (Lesnoff and Lancelot 2012) if the data were over-dispersed. To test changes in adult behaviours, we included the two experimental conditions (enriched and control) as a fixed factor and individual ID as a random factor to avoid pseudo-replication. We ran the analysis separately for each behavioural category. We used GLM and the *glm* function with a Poisson distribution to analyse infant behaviours, using the experimental condition as a fixed factor. We compared the models with and without the parameters mentioned above based on the likelihood ratio test with approximate chi-squared distribution (Kubo 2012).

Results

Study 1: Introducing tool-based devices

Study 1-1: Tool-using behaviours of adult chimpanzees
All adult chimpanzees could use the dipping feeder from the outset. Two of the five chimpanzees mastered at least the first level of pounding feeder use (day 6 for Suzumi and day 18 for Koiko). Both of the successful chimpanzees were female, and both initially tried to fish the contents out of the feeder, but later changed their behaviour to pounding. Only Suzumi progressed to the third level. Her tool lengths increased significantly over the course of study 1, regardless of the difficulty level (Fig. 2, S2: $\chi^2 = 2.71$, $p < 0.05$). Koiko could not get food from the level 2 and 3 feeders, though she tried to do so. The two successful chimpanzees could flexibly choose tools for the dipping feeders as they showed lower rates of changing tools for dipping feeders, sometimes bringing tools

Table 3. Results of study 1-1.

Name	Pounding feeders	Dipping feeders: Dipping rate (sec)	Dipping feeders: Ratio of bringing tools	Dipping feeders: Tool change / dipping bout	Feeding motivation	Computer-based cognitive tasks
Suzumi	Level 1, 2, 3	359.3	0.186	1.26	0.138	9
Koiko	Level 1	453.2	0.276	1.19	0.141	6
James	-	578.2	0.036	2.33	0.102	7
Takashi	-	29.6	0	1.33	0.236	12
Niini	NA	NA	NA	NA	NA	3

Note. The column for pounding feeders shows the levels of feeders from which the individuals could obtain food. Data of computer-based cognitive tasks derive from Tanaka et al. (2015). The number represents the maximum number of numerals that the individual could identify in correct order in the numerical sequence tasks (Matsuzawa et al. 2006). For example, Takashi could touch numerals appearing on a screen from 1 to 12 in order.

from beyond reaching distance (Table 3). Individual differences in performance were not explained by the rate of tool use, the feeding motivation, as assessed by the rate of foraging normal food under the control condition in study 2, or cognitive ability, as assessed by a computer-based touch-panel screen.

Although Suzumi could obtain 3-cm-sized food from the level 3 feeder, the effort did not continue for long. Thus, we decreased the food size to about 1.5 cm (similar to the hole size used for whole food) for study 2.

Study 1-2: Acquisition of tool use in an infant chimpanzee

The infant acquired tool use at the age of 19 months, between the two study phases. Peering behaviours directed by the infant toward the adults were observed more frequently than those by adults (Fig. 3-a; $\chi^2 = 9.29$, $p < 0.01$). During study 2, he tended to observe adult behaviours more often after he failed to obtain juice than after he succeeded (Fig. 3-b; $\chi^2 = 9.36$, $p < 0.05$).

Study 2

Study 2-1: Effects on adult behaviours and use of space

All of the adult chimpanzees used at least one of the feeders. The rates of self-directed behaviours and abnormal behaviours decreased when the tool use devices were provided (Fig. 4a: self-directed behaviours: $\chi^2 = 18.02$, $p < 0.001$; abnormal behaviours, $\chi^2 = 18.86$, $p < 0.001$), although abnormal behaviours were rare in this group of chimpanzees. Time spent moving, foraging, inactive, and engaging in social behaviours did not change (move: $\chi^2 = 2.97$, $p = 0.084$; forage: $\chi^2 = 0.252$, $p = 0.617$; inactive: $\chi^2 = 2.71$, $p = 0.1$; affiliative social: $\chi^2 = 2.45$, $p = 0.118$). There was no evidence of habituation, as there was no significant change in the rate of using the feeders between the earlier and later half of the study ($\chi^2 = 0.161$, $p = 0.689$).

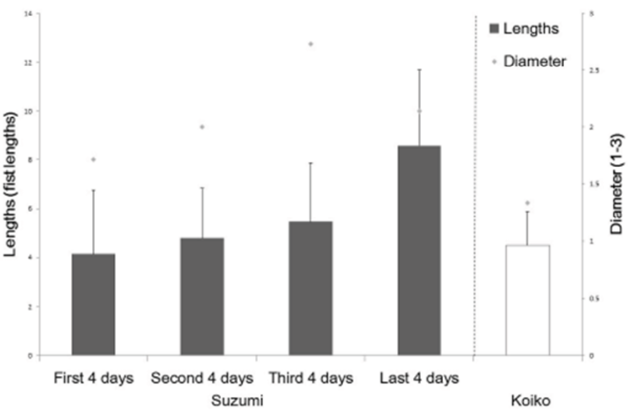

Figure 2. Changes in tool lengths and widths. One of the successful females (Suzumi) increased the length of tools over the course of the study. The error bars indicate the standard errors of means.

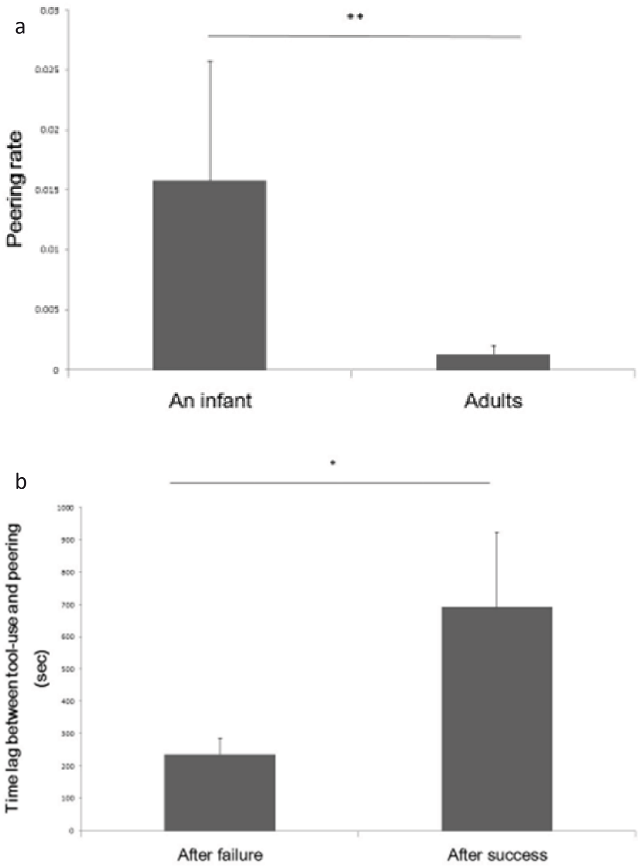

Figure 3. (a) Peering behaviours in adult and infant chimpanzees; (b) peering behaviours and tool-use of an infant chimpanzee. The infant observed others' behaviours more often than did the adults (Fig. 3a). During study period 2, the infant peered at adults 31 times. He tended to peer at adult behaviours more after his failures (Fig. 3b). The error bars indicate the standard errors of means. Significant differences between conditions are indicated (** $p < 0.01$).

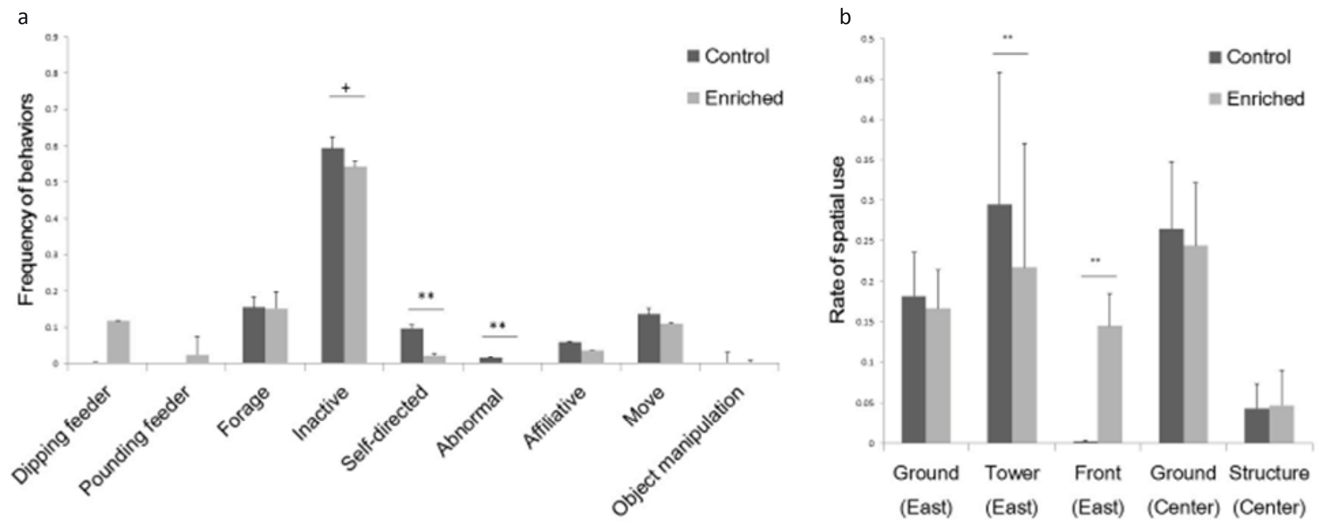

Figure 4. Changes in (a) behaviour and (b) use of space in adult chimpanzees. The error bars indicate the standard errors of means between individuals. Significant differences between conditions are indicated (** $p < 0.01$, * $p < 0.05$).

The use of space changed with the enriched condition, but only in the east enclosure, where the devices were deployed. The chimpanzees increased their use of the front parts and decreased their use of the tower, although the proportion of time spent on the ground in the east enclosure was unchanged (Fig. 4b: front: $\chi^2 = 235.5$, $p < 0.001$; tower: $\chi^2 = 28.53$, $p < 0.01$; ground: $\chi^2 = 0.615$, $p = 0.433$). There was no change in the spatial use of the central ground (structure: $\chi^2 = 2.547$, $p = 0.111$; ground: $\chi^2 = 0.724$, $p = 0.395$).

Study 2-2: Effects on infant behaviours and use of space

The time spent inactive by the infant decreased, and the object manipulation time increased under the control condition (Fig. 5a: inactive: $\chi^2 = 4.09$, $p = 0.0431$; object manipulation: $\chi^2 = 5.812$, $p = 0.0159$). The infant showed almost no self-directed behaviours or abnormal behaviours, and the other behaviours did not change (move: $\chi^2 = 0.109$, $p = 0.741$; forage: $\chi^2 = 0.134$, $p = 0.714$; affiliative social: $\chi^2 = 2.72$, $p = 0.092$). The use of space showed similar trends to those of the adults in both the east compound (Fig. 5b: front: $\chi^2 = 33.88$, $p < 0.001$; tower: $\chi^2 = 3.33$, $p = 0.0682$; ground: $\chi^2 = 1.07$, $p = 0.301$) and the central ground (structure: $\chi^2 = 0.812$, $p = 0.367$; ground: $\chi^2 = 0.00437$, $p = 0.947$).

Discussion

The two types of feeders facilitated tool-using behaviours in all of these chimpanzees. The feeders not only increased tool-using behaviours but also decreased self-directed behaviours and abnormal behaviours. Our results are consistent with previous studies (Celli et al. 2003; Clark and Smith 2013), which showed that tool-based devices increased species-specific foraging behaviours. Notably, the effects were evident even in the already relatively enriched zoo environment. The outdoor enclosure of the zoo in this study contained various types of plants, and foods were scattered around the enclosures. Chimpanzees used the tool-based devices even though they had other choices, and they showed no evidence of habituation. Space use was also changed significantly. When the feeders were available, the chimpanzees spent more time near the feeders and less time in the tower in the

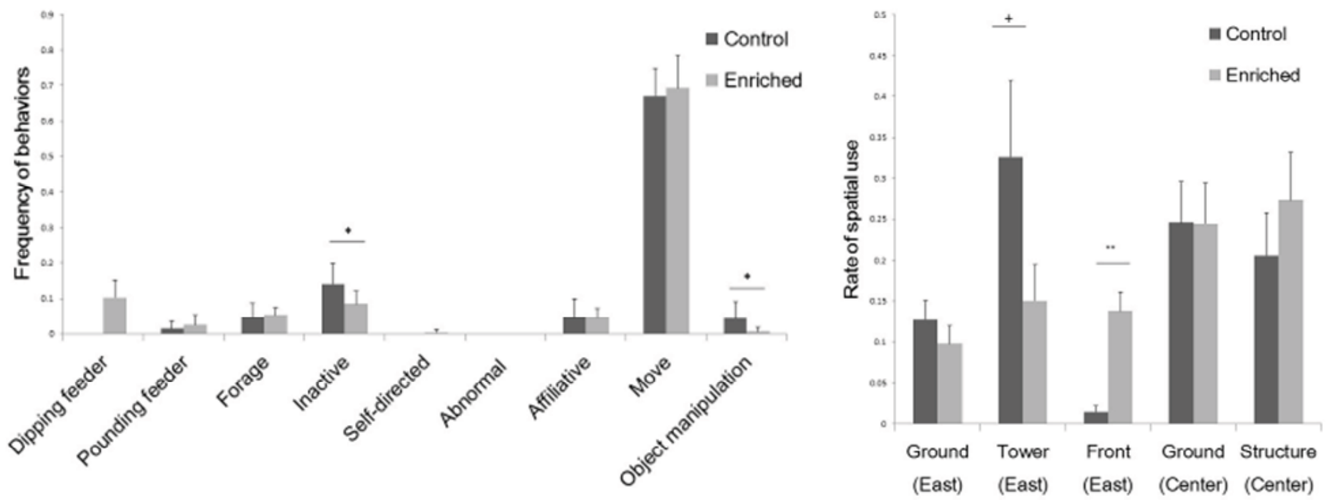

Figure 5. Changes in (a) behaviour and (b) use of space in an infant chimpanzee. The error bars indicate the standard errors of means. Significant differences between conditions are indicated (** $p < 0.01$, * $p < 0.05$).

east ground; these changes in enclosure use were seen only in the east ground, where the feeders were available, while there was no significant change in the use of space in the adjacent enclosure.

This intervention showed that chimpanzees can spontaneously invent new tool-using behaviours, including new motor patterns, even in adulthood. Two chimpanzees invented techniques for using the feeders, and one also varied the length of tools. Flexibility in chimpanzee behaviour is widely known and researchers have sometimes witnessed novel behaviours in wild chimpanzee populations (Biro et al. 2003; Toshisada Nishida et al. 2009). However, most of the novel behavioural patterns were adaptations of existing skills to novel targets. Although simple techniques are learned rapidly by adult captive chimpanzees (Hopper et al. 2007; Whiten et al. 2005), acquisition of behaviours with complex motor patterns in adulthood seems to be difficult (Hayashi et al. 2005). The difficulty of acquiring behaviours that require new motor patterns may be related to the fact that chimpanzees pay less attention to others' or their own actions in cases of imitation or when they are monitoring their own actions (Kaneko and Tomonaga 2014; Myowa-Yamakoshi 2006). Meehan and Mench (2007) pointed out the importance of providing the appropriate level of challenge. They defined an appropriate challenge as "problems that may elicit frustration, but are potentially solvable or escapable through the application of cognitive and behavioural skills". Considering the difficulty of acquiring new tool-using behaviours and their gradual adaptation, our intervention may be considered an appropriate cognitive challenge.

There were individual differences in behavioural acquisition. The two female chimpanzees who flexibly selected tools for the dipping feeders, showing a lower tool-changing rate and a higher ratio of using tools outside their reaching distance, were able to acquire the new skills. This was not consistent with their abilities in cognitive tasks using a touch-panel screen (Tanaka et al. 2015). These results indicate consistency in tool-using ability within the study subjects, but this was not consistent with their ability in serial learning tasks. In addition, the ability to acquire new behavioural patterns was not related to feeding motivation, rate of tool use, or rearing history. The changes in self-directed behaviours in study 2 were larger in the skilled chimpanzees. Lonsdorf et al. (2004) suggested sex differences in the acquisition of tool-using behaviours in wild chimpanzees. In that study, females tended to learn ant-fishing behaviours faster than males. Likewise, we found that females mastered new tool-using behaviours faster than males. Further studies are needed to elucidate the factors underlying such individual differences and clarify how they relate to individual welfare.

We further showed the effects of feeders on an infant's behaviour. The age of the infant's first tool use was comparable to previous reports (Hayashi and Matsuzawa 2003; Hirata and Celli 2003). Inactive time decreased under the enriched conditions. The infant frequently observed adult behaviours and increased his own "unnecessary" tool use under the control condition, which may reflect his high motivation toward tool use. Furthermore, he tended to watch the others' behaviours more often after bouts in which he failed to obtain juice. Although previous studies suggested that cognitive challenge can cause mild stress, especially when subjects fail to obtain rewards (Yamanashi and Matsuzawa 2010), such failure may be important in facilitating learning. Kendal et al. (2015) reported that adult chimpanzees are more likely to rely on social information when uncertain. Similar cognitive processes might underlie both adult and infant learning. Cognitive enrichment may also provide good opportunities to study a species' process of behavioural acquisition and its underlying cognitive mechanisms.

Overall, the devices assessed here could facilitate tool use among zoo-housed captive chimpanzees, although the advantages of the two feeders differed. The dipping feeders increased the duration of tool use by various individuals, whereas the pounding feeders represented a more challenging task for the chimpanzees. In the future, we will improve the pounding feeders with the aim of efficiently increasing tool use.

Supplementary materials

Video S1: Use of two types of feeders by chimpanzees
https://www.youtube.com/watch?v=64YeQNIRJMg
Video S2: Suzumi's change of the techniques and tools
http://youtu.be/y_DCQBq9_m8

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